SUCCESSION IN PINYON-JUNIPER WOODLANDS FOLLOWING WILDFIRE IN THE GREAT BASIN

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ABSTRACT.— Twenty-one areas in pinyon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodlands burned by wildfire from approximately 1 to 60 years prior to sampling and adjacent unburned mature woodland stands were studied in Nevada and California to determine successional patterns and individual species responses to burning and to changing plant communities through time. One year after burning, all late successional woodland species were present in postburn plant communities except tree species. Increases in both cover and occurrence of annual and perennial forbs resulted in their dominance on early successional sites. Shrubs and annual grasses dominated midsuccessional sites, subsequently giving way to tree, shrub, and perennial grass dominance in late succession. North and east slopes generally supported high cover and occurrence of shrubs, perennial grasses, and perennial forbs, and south and west slopes generally supported high cover and occurrence of annual forbs and annual grasses. The ability to group species according to preferential occurrence on various aspects and successional stages can be used to predict plant community composition in time and space in the pinyon-juniper woodlands.

Fire is a natural component of the pinyon-juniper woodland and a primary cause of secondary succession. Everett and Ward (1984) and Klebenow and others (1977) described patterns of early succession following prescribed burns on sites in eastern Nevada. Barney and Frischknecht (1974) examined 28 Utah sites primarily in juniper-dominated woodlands burned by wildfire from 3 to over 100 years ago. Within the framework of a larger study, Stager (1977) described plant species variation among wildfire sites in Great Basin woodlands dominated by both pinyon and juniper. Seven sites were studied, ranging in postburn age from 2 to 115 years. The ability to predict postfire plant and plant community response in the pinyon-juniper woodland depends upon a broader data base than is currently available.

This study was designed to increase our knowledge of individual species response to fire in Great Basin pinyon-juniper woodlands and subsequent changes in cover and occurrence through time. Variations of species cover and occurrence among aspects and differences in the successional cycle between aspect groups were also examined.

FIELD METHODS AND DATA ANALYSIS

In 1981 and 1982 we found 21 areas burned by wildfire from approximately 1 to 60 years ago in pinyon-juniper woodlands in Nevada and California (Table 1). Eight of the burns had been seeded following burning (Koniak 1983). Four successional stages were apparent among the burns: early succession (1-year-old burns), early midsuccession (4- to 8-year-old burns), midsuccession (15- to 17-year-old burns), and late midsuccession (22- to 60-year-old burns). Adjacent to each burned area, unburned pinyon-juniper represented the late successional stage. Study sites were limited to areas that had had a minimum 100 trees per hectare.

On each burn, the entire area or a representative part of the burn was surveyed to determine the plant communities present. A sample stand or relevé was established in each plant community, with size varying with the size of the sampled community. Relevé size generally ranged from 20 m^2 to 100 m^2. Each relevé had to be large enough to contain all species in the plant community and had to have uniform aspect and slope and homogeneous plant cover. On each relevé all species were recorded, and canopy cover for each individual species as well as each growth form (i.e., annual forb, perennial forb, annual grass, perennial grass, shrub, tree) was estimated according to the Braun-Blanquet cover abundance scale (Mueller-Dombois and El-

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TABLE 1. Description of 21 pinyon-juniper burned areas in Nevada (NV) and California (CA) studied to determine successional patterns.

Study areas	Date of burn	Location description	Average elevation (m)	Average annual precipitation (cm)
Double Springs (NV)	1920's	T11N R21E Sec 31, 32	1975	33
June Ellen (NV)	1950's	T15N R21E Sec 35	2060	33
Jumbo (NV)	7-57	T17N R20E Sec 23,26	1900	33
War Canyon (NV)	8-58	T20N R36E Sec 25	2160	30
Jake Hill (NV)	7-59	T11N R21E Sec 5	1665	20
Big Creek #1 (NV)	8-64	T17N R43E Sec 10,15,16	2220	30
Gabbs (NV)	8-64	T12N R37E Sec 29	2135	30
Bald Mountain (NV)	7-65	T23N R57E Sec 4,9	2190	32
Wichman Canyon (NV)	7-65	T 8N R27E Sec 19,20,30	2050	24
Bennett Crossing (NV)	5-66	T12N R22E Sec 20	2025	33
Milk Ranch (NV)	8-70	T 8N R65E Sec 19,20	2100	33
Pine Nuts (NV)	8-73	T11N R22E Sec 7,18,19,30		
		T11N R23E Sec 13,24,25,36	2060	33
Rock Creek (CA)	7-73	T 8N R23E Sec 17,24	1920	24
China Gardens (CA)	7-74	T 7N R23E Sec 4,5		
		T 8N R23E Sec 28,29,32,33	1910	24
Mt. Wilson (NV)	7-74	T 4N R68E Sec 1–3,10–15		
		Sec 21–28	2185	33
Geiger Grade (NV)	9-74	T18N R20E Sec 35,36	1797	33
Miller (NV)	7-76	T19N R61E Sec 24–26	2110	31
Big Creek #2 (NV)	8-77	T17N R43E Sec 9	2110	30
Rock Springs (NV)	7-81	T19N R61E Sec 34,35	2230	31
Austin (NV)	8-81	T19N R43E Sec 25,36		
		T19N R44E Sec 30,31	2020	30
Slater Mine (NV)	8-81	T12N R21E Sec 4–8	2230	31

lenberg 1974). Elevation, slope, and aspect were recorded.

Unburned pinyon-juniper stands were sampled by the same methods used for sampling the burned stands. Several tree cores were taken in each of the 21 areas, with the average age for each area ranging from 72 to 159 years. Approximately one unburned relevé was sampled for every four burned relevés. A total of 546 relevés, 433 burned and 113 unburned, were sampled. There were 187 species in the entire sample.

Chi-square tests were used to delineate the relationships of individual species to aspect and age of stands and to compare the eight seeded burns and 13 nonseeded burns.

RESULTS AND DISCUSSION

Big sagebrush (*Artemisia tridentata*) was the only species found on all 21 burns sampled (Table 2). All the following were found on 75% or more of the burns sampled: rubber rabbitbrush (*Chrysothamnus nauseosus*), low rabbitbrush (*Chrysothamnus viscidiflorus*), a telope bitterbrush (*Purshia tridentata*), desert gooseberry (*Ribes velutinum*), cheatgrass (*Bromus tectorum*), Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Sitanion hystrix*), prickly poppy (*Argemone munita*), tapertip hawksbeard (*Crepis acuminata*), and tailcup lupine (*Lupinus caudatus*). All except prickly poppy were also present on mature woodlands. These species occurred over a wide range of successional stages and locations, indicating a wide ecological amplitude. Individual species cover was generally less than 1% on most releves. Only 19 understory species had $\geq$ 5% cover on more than 5% of the relevés where the species occurred (Table 3). Cover will only be discussed if it varies substantially from occurrence values (occurrence = number of sites where a species occurred per total number of sites).

First-Year Postfire Species Response

Initial responses to fire were determined by comparing occurrence and cover of individual species on mature woodlands and on one-

TABLE 2. Plant species that occur on ≥ 5 (24%) of the 21 burns sampled.

Scientific name[1]	Common name	Constancy[2]
Trees and shrubs		
Pinus monophylla	Single leaf pinyon	33
Amelanchier alnifolia	Saskatoon serviceberry	29
Artemisia tridentata	Big sagebrush	100
Ceanothus velutinus	Snowbrush ceanothus	24
Chrysothamnus nauseosus	Rubber rabbitbrush	86
Chrysothamnus viscidiflorus	Low rabbitbrush	95
Ephedra viridis	Green ephedra	67
Opuntia spp.	Prickly pear	33
Prunus andersonii	Anderson peachbrush	43
Purshia tridentata	Antelope bitterbrush	76
Ribes velutinum	Desert gooseberry	95
Sambucus cerulea	Blueberry elder	52
Symphoricarpos oreophilus	Mountain snowberry	57
Tetradymia canescens	Gray horsebrush	38
Xanthocephalum sarothrae	Broom snakeweed	24
Grasses		
Agropyron spicatum	Bluebunch wheatgrass	29
Bromus tectorum	Cheatgrass brome	95
Elymus cinereus	Great Basin wild rye	52
Festuca idahoensis	Idaho fescue	24
Oryzopsis hymenoides	Indian ricegrass	57
Poa fendleriana	Mutton bluegrass	52
Poa secunda	Sandberg bluegrass	95
Sitanion hystrix	Bottlebrush squirreltail	90
Stipa comata	Needle-and-thread	43
Stipa speciosus	Desert needlegrass	24
Stipa thurberiana	Thurber needlegrass	71
Perennial forbs		
Antennaria rosea	Rose pussytoes	29
Arabis holboellii	Holboell rockcress	67
Arenaria nuttallii	—	24
Argemone munita	Hedgehog prickly poppy	76
Astragalus beckwithii	Beckwith milkvetch	43
Astragalus filipes	—	29
Astragalus purshii	Pursh locoweed	52
Balsamorhiza hookeri	Hooker balsamroot	24
Balsamorhiza sagittata	Arrowleaf balsamroot	52
Calochortus nuttallii	Segolily	33
Castilleja chromosa	Indian paintbrush	38
Chaenactis douglasii	Douglas chaenactis	71
Crepis acuminata	Tapertip hawksbeard	76
Cryptantha flavoculata	Roughseed cryptantha	24
Delphinium andersonii	Anderson larkspur	28
Erigeron aphanactis	Hairy fleabane	33
Eriogonum elatum	—	29
Eriogonum umbellatum	Sulphur eriogonum	52
Galium multiflorum	Shrubby bedstraw	29
Lithosperum ruderale	Wayside gromwell	24
Lomatium nevadense	Nevada lomatium	29
Lupinus caudatus	Tailcup lupine	76
Lygodesmia spinosa	Thorn skeleton plant	67
Machaeranthera canescens	Hoary aster	71
Penstemon deustus	Scabland penstemon	29
Penstemon speciosus	Royal penstemon	48
Phacelia hastata	—	57
Phlox hoodii	Hood's phlox	38
Phlox spp.	—	57
Phoenicaulis cheiranthoides	Wallflower phoenicaulis	24

TABLE 2. continued.

Scientific name[1]	Common name	Constancy[2]
Senecio integerrimus	Lambstongue groundsel	29
Senecio multilobatus	Lobeleaf groundsel	29
Zigadensus paniculatus	Foothill deathcamas	24
Annual forbs		
Collinsia parviflora	Little flower collinsia	29
Cryptantha spp.	—	38
Descurainia spp.	Tansy mustard	38
Eriastrum sparsiflorum	Eriastrum	43
Eriogonum spp.	—	33
Erodium cicutarium	Alfileria	33
Gayophytum spp.	Groundsmoke	38
Gilia spp.	—	43
Lactuca serriola	Prickly lettuce	33
Lappula occidentalis	Annual stickweed	33
Mentzelia albicaulis	White stem mentzelia	48
Microsteris gracilis	—	24
Nicotiana attenuata	Coyote tobacco	24
Salsola iberica	Saltwort	29
Sisymbrium altissimum	Tumble mustard	62
Seeded species		
Agropyron cristatum	Fairway wheatgrass	33
Agropyron intermedium	Intermediate wheatgrass	29

[1]According to Holmgren and Reveal (1966).
[2]Constancy is defined as the number of burns a species occurred on divided by the total number of burns.

TABLE 3. Occurrence (percent of relevés a species occurs on) and cover (percent of the relevés a species occurs on that has ≥ 5% cover) of species[1] on five successional stages.

	Occurrence Successional stages					Cover[2] Successional stages				
	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Tree species										
Juniperus osteosperma	0^{c}	0^{c}	2^{c}	27^{b}	56^{a}	0^{b}	0^{b}	0^{b}	0^{b}	100^{a}
Pinus monophylla	0^{c}	$.5^{c}$	5^{c}	80^{b}	100^{a}	0^{b}	0^{b}	0^{b}	5^{b}	100^{a}
Shrub species										
Artemisia tridentata	9^{c}	74^{b}	79^{b}	98^{a}	88^{ab}	0^{d}	15^{c}	36^{b}	88^{a}	30^{b}
Chrysothamnus nauseosus	2^{b}	66^{a}	63^{a}	65^{a}	8^{b}	0^{b}	10^{b}	49^{a}	32^{a}	0^{b}
Chrysothamnus viscidiflorus	37^{c}	54^{b}	75^{a}	44^{bc}	22^{d}	6^{c}	21^{b}	33^{a}	0^{c}	0^{c}
Ephedra viridis	17^{b}	52^{a}	68^{a}	60^{a}	51^{a}	—	—	—	—	—
Prunus andersonii	1^{d}	35^{b}	67^{a}	31^{b}	13^{c}	—	—	—	—	—
Purshia tridentata	28^{c}	60^{b}	61^{b}	83^{a}	73^{a}	0^{c}	3^{c}	15^{c}	45^{a}	24^{b}
Ribes velutinum	25^{c}	72^{a}	48^{b}	59^{ab}	56^{b}	—	—	—	—	—
Sambucus cerulea	45^{ab}	28^{b}	30^{b}	63^{a}	4^{c}	—	—	—	—	—
Symphoricarpos oreophilus	39^{a}	27^{ab}	22^{ab}	38^{a}	20^{b}	6^{bc}	47^{a}	18^{ab}	0^{c}	29^{a}
Tetradymia canescens	8^{b}	37^{a}	10^{b}	4^{b}	13^{b}	0^{b}	22^{a}	0^{b}	0^{b}	0^{b}
Grasses										
Bromus tectorum	42^{c}	86^{a}	61^{b}	60^{b}	49^{bc}	13^{c}	76^{a}	71^{b}	48^{b}	7^{c}
Festuca idahoensis[3]	44^{a}	—	—	—	19^{b}	0^{b}	—	—	—	33^{a}
Oryzopsis hymenoides	12^{bc}	22^{b}	56^{a}	16^{bc}	8^{c}	—	—	—	—	—
Poa fendleriana	4^{c}	7^{c}	7^{bc}	31^{a}	17^{ab}	—	—	—	—	—
Poa secunda	75^{a}	19^{c}	39^{b}	49^{b}	63^{a}	—	—	—	—	—
Sitanion hystrix	43^{c}	58^{b}	49^{bc}	90^{a}	44^{c}	3^{b}	15^{a}	28^{a}	0^{b}	0^{b}
Stipa thurberiana	33^{b}	12^{c}	37^{ab}	57^{a}	34^{b}	0^{bc}	9^{b}	23^{a}	21^{a}	3^{bc}
Perennial forbs										
Arabis holboellii	19^{b}	9^{c}	26^{b}	26^{b}	50^{a}	—	—	—	—	—

TABLE 3. continued.

	Occurrence Successional stages					Cover[2] Successional stages				
	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Argemone munita	44^{ab}	56^{a}	26^{b}	31^{b}	0^{c}	2^{b}	8^{a}	0^{b}	0^{b}	0^{b}
Astragalus purshii	14^{b}	6^{b}	33^{a}	14^{b}	8^{b}	—	—	—	—	—
Balsamorhiza sagittata	21^{a}	29^{a}	20^{ab}	11^{b}	19^{ab}	—	—	—	—	—
Chaenactis douglasii	8^{a}	7^{a}	16^{a}	13^{a}	7^{a}	—	—	—	—	—
Crepis acuminata	40^{a}	24^{b}	29^{b}	36^{ab}	13^{c}	5^{ab}	6^{ab}	16^{a}	0^{b}	0^{b}
Eriogonum umbellatum	5^{ab}	4^{b}	11^{a}	5^{ab}	10^{a}	—	—	—	—	—
Lupinus caudatus	46^{a}	20^{c}	32^{ab}	25^{ab}	19^{bc}	9^{ab}	7^{ab}	0^{b}	13^{a}	0^{b}
Lygodesmia spinosa	31^{a}	32^{a}	19^{ab}	27^{a}	13^{b}	—	—	—	—	—
Machaeranthera canescens	18^{a}	15^{a}	19^{a}	28^{a}	6^{b}	—	—	—	—	—
Phacelia hastata	47^{a}	36^{a}	48^{a}	15^{b}	3^{c}	—	—	—	—	—
Phlox hoodii	66^{a}	6^{c}	45^{b}	0^{c}	32^{b}	—	—	—	—	—
Phlox spp.	26^{a}	13^{b}	23^{ab}	31^{a}	12^{b}	—	—	—	—	—
Annual forbs										
Collinsia parviflora	56^{a}	1^{d}	0^{d}	6^{c}	27^{b}	—	—	—	—	—
Cryptantha spp.	56^{a}	12^{b}	0^{b}	0^{b}	11^{b}	11^{a}	0^{b}	0^{b}	0^{b}	0^{b}
Descurainia spp.	37^{a}	7^{b}	3^{bc}	0^{c}	23^{a}	—	—	—	—	—
Eriogonum spp.	1^{c}	33^{a}	8^{ab}	0^{c}	6^{b}	—	—	—	—	—
Erodium cicutarium	0^{b}	25^{a}	25^{a}	20^{a}	0^{b}	0^{b}	3^{b}	0^{b}	60^{a}	0^{b}
Gayophytum spp.	57^{a}	10^{c}	11^{bc}	29^{b}	6^{c}	—	—	—	—	—
Gilia spp.	65^{a}	4^{c}	2^{c}	46^{ab}	34^{b}	58^{a}	0^{b}	0^{b}	0^{b}	0^{b}
Lactuca serriola	25^{a}	7^{b}	10^{b}	0^{b}	0^{b}	—	—	—	—	—
Mentzelia albicaulis	32^{a}	35^{a}	0^{c}	8^{b}	2^{bc}	—	—	—	—	—
Nicotiana attenuata	38^{a}	4^{b}	0^{b}	0^{b}	0^{b}	—	—	—	—	—
Sisymbrium altissimum	7^{b}	46^{a}	35^{a}	12^{b}	4^{b}	0^{b}	35^{a}	21^{a}	0^{b}	0^{b}

[1]Species that occurred on ≥ 20% of the total relevés or ≥ 20% of the relevés in any one of the categories examined.
[2]Only species that occurred on ≥ 5% of the actual relevés the species occurs on with ≥ 5% cover were examined.
[3]Chi square test including all successional stages was not valid, therefore, only early and late stages were compared.

year-old burns (Table 3). Tree species were essentially eliminated by burning. Shrubs such as big sagebrush and bitterbrush, which regenerate by seed, were easily killed by burning but began to reoccupy some burned sites within one year. Reestablishment of big sagebrush appeared to occur through migration and germination of seed from adjacent unburned areas or germination of on-site soil seed reserves. Bitterbrush reestablished primarily by germination of rodent caches (pers. obs.). Ecotypes of bitterbrush that can resprout were not found on the study sites. Both species had negligible cover on one-year-old burns.

Although some individual plants were killed, all root-sprouting species studied remained part of the postburn plant community. This is consistent with other studies (Wright et al. 1979). Occurrence of rubber rabbitbrush and horsebrush (*Tetradymia canescens*) was not significantly different between mature woodland stands and one-year-old burns. One-year-old wildfire sites had significantly higher occurrences of blueberry elder (*Sambucus cerula*), mountain snowberry (*Symphoricarpos orephilus*), and low rabbitbrush than did mature woodlands and significantly lower occurrences of Mormon tea (*Ephedra viridis*), desert gooseberry, and Anderson peachbrush (*Prunus andersonii*). Only mountain snowberry and low rabbitbrush occurred on early postburn sites with cover values ≥ 5%. Even though occurrence of mountain snowberry was significantly greater on the one-year-old burns than on the woodland stands, the percent of these relevés with cover ≥ 5% was significantly less on one-year-old burns. The differences were not significant between the two successional stages for low rabbitbrush.

Root crowns of most perennial grasses can survive wildfire, continuing growth when conditions are favorable (Wright et al. 1979, White and Currie 1983). Comparison of one-year-old burns and mature woodlands showed that only the occurrence of one species, mutton bluegrass (*Poa fendleriana*), was signifi-

cantly reduced. Occurrence of other perennial grasses remained the same or increased slightly. For most perennial grasses, high cover values (≥ 5%) were not found on either one-year-old burns or mature woodlands. Idaho fescue (*Festuca idahoensis*) occurred on the highest number of relevés, all on mature woodlands, with cover ≥ 5%. Cheatgrass, an annual grass, was killed by wildfire but regained postburn levels of occurrence and cover within one year from germination of either soil seed reserves or seed from adjacent areas (Young and others 1976, Merrill and others 1980).

Most perennial forbs occurred more frequently on one-year-old burns than on mature woodlands. Only Holboell rockcress (*Arabis holboellii*) had significantly lower occurrence on the early successional stage than on the late stage. Few relevés had cover values ≥ 5% for any perennial forb species. No significant differences occurred between cover values of the two stages, although cover tended to be higher on one-year-old burns.

Annual forbs are killed by burning but rapidly reoccupy most sites by germination of seed from adjacent unburned areas or on site soil seed reserves (Koniak and Everett 1982). Occurrence of most annual forbs was significantly greater on one-year-old burns than on mature woodlands. Only gilia (*Gilia* spp.) and cryptantha (*Cryptantha* spp.) occurred with cover ≥ 5% and only on the one-year-old burns.

Occurrence and cover of understory species in pinyon-juniper woodlands generally remained the same or increased after burning. High postfire occurrence or cover of perennial species may be attributed to a combination of high tolerances to burning, increased visibility of plants from either increased size or elimination of litter or duff, and increased germination, survival, and growth following release from competition from late successional species. High postfire occurrence or cover of annual species may result from increased germination and growth of on-site seed or seeds from adjacent unburned sites.

Several shrub species and Holboell rockcress decreased substantially after fire. The decrease may be attributed to a high susceptibility to fire-related injury and death, to the inability to compete with early successional species or, for woody species, to the slow accumulation of biomass. Wildlife grazing may also contribute to the decline in a number of browse species.

Species Variation over Five Successional Stages

Annual forbs displayed the greatest variation in distribution patterns among successional stages (Table 3). Some species occurred most frequently on early successional sites, others occurred most frequently on midsuccessional sites, and still others had higher occurrence on early and late sites than on midsuccessional sites. Most perennial forbs were found on a disproportionately higher number of early and midsuccessional sites than on late sites. Hood's phlox (*Phlox hoodii*) had significantly greater occurrence on the early successional stage than on later stages, but occurrence was also high during midsuccession and late succession. Holboell rockcress was the only nontree species that occurred more frequently on late successional sites than at other stages.

Perennial and annual grasses were consistently found on more mid-successional sites than on early or late sites. A notable exception was Sandberg bluegrass, whose high occurrence on early and late successional sites paralleled the distribution patterns of several annual forbs.

All shrubs, except blueberry elder and mountain snowberry, had relatively low occurrence on early successional sites compared to midsuccessional sites. Occurrence of all root sprouting shrubs, except desert gooseberry and Mormon tea, decreased between midsuccession and late succession. Big sagebrush and antelope bitterbrush, shrub species that regenerate by seed, maintained high occurrence throughout midsuccession and late succession. Unlike occurrence, cover of antelope bitterbrush and big sagebrush decreased significantly from midsuccession to late succession. Apparently, as tree species dominated a site, the resources available to understory species rapidly diminished and cover was greatly reduced.

Tree species began to reestablish 20 to 30 years after fire, but cover was minimal even 60

TABLE 4. Aspects on which species[1] occurred most frequently.

Species	Aspect			
	North	East	South	West
Shrubs				
* *Artemisia tridentata*	X	X		X
Chrysothamnus nauseosus				X
* *Chrysothamnus viscidiflorus*	X	X		
Ephedra viridis			X	X
* *Prunus andersonii*		X		
* *Purshia tridentata*	X	X		X
* *Ribes velutinum*	X	X		
* *Symphoricarpos oreophilus*	X	X		
* *Tetradymia canescens*	X	X		X
Grasses				
* *Bromus tectorum*				X
* *Festuca idahoensis*	X	X		
Oryzopsis hymenoides		X		
* *Poa fendleriana*		X		
Poa secunda		X	X	XX[2]
Sitanion hystrix		X	X	XX
* *Stipa thurberiana*		X		
Perennial forbs				
Argemone munita	X	X	X	X
* *Arabis holboellii*	X			
Astragalus purshii	X	X	X	X
* *Balsamorhiza sagittata*	X	X		
* *Crepis acuminata*	X	X		
Eriogonum elatum	X	X		
* *Eriogonum umbellatum*	X	X		
* *Lupinus caudatus*	X	X		
Lygodesmia spinosa	X	X		
* *Machaeranthera canescens*	X	X		
* *Phacelia hastata*			X	X
Phlox hoodii	X	X		X
Phlox spp.	X	X	X	X
Annual forbs				
Collinsia parviflora		X		
Cryptantha spp.	X	X	X	X
* *Descurainia* spp.			X	X
Eriogonum spp.	X	X		
* *Erodium cicutarium*			X	X
Gayophytum spp.			X	X
* *Gilia* spp.			X	X
Lactuca serriola			X	X
Mentzilia albicaulus			X	X
Nicotiana attenuata	X	X	X	X
* *Sisymbrium altissimum*			X	X

[1]Species that occurred on ≥ 20% of the relevés in any one of the categories investigated (i.e., north, south, east, west).
[2]Occurrence of species with X's in all categories was not significantly different among aspects.
*Differences are significant at $P < .05$.

years after burning. Recent work (Tausch and West, in prep.) indicates that at this point trees rapidly increase in density and cover, dominating a site 100 to 150 years after burning.

Species with high occurrence in early succession apparently survived wildfire as seeds on the burned site or on adjacent unburned sites, or as buds at the root crowns, or both. They were able to rapidly take advantage of the increased availability of water, nutrients, and light in the postfire environment. Limited occurrence of species in midsuccessional or late stages may be related to several factors (Barbour et al. 1980). Seed may germinate most effectively after fire scarification. As

shrubs and later tree species overtop the low-growing herbaceous forbs, reducing the light intensity at the soil level, photosynthesis is reduced and shade-intolerant plants will not survive. Competition with midsuccessional or late species for water and nutrients may limit occurrence of some species. Plants prominent in later stages of succession may produce allelopathic chemicals that may inhibit growth of other plants. Increase in occurrence of perennial species in midsuccession may be correlated to the attainment of the critical biomass necessary for seed production or to the increase in ground cover providing a favorable microsite for seed germination and plant survival.

Reentry of tree species into the plant community depends upon perennial nurse plants associated with midsuccessional and late stages (Everett and Ward 1984). Nontree species with high occurrence on late stages can successfully compete with other late species and may actually benefit from the combination of shade and relative lack of ground cover. However, many of these species exhibit a substantial reduction in cover with increasing tree dominance.

Common factors may explain similar species occurrence on two seemingly dissimilar sites, one-year-old burns (early succession) and mature woodlands (late succession): an abundance of bare ground and a lack of competition for resources in the upper soil horizons. Species in this group appear to be tolerant of late successional conditions (shade, tree competition, alleopathy) but cannot compete with species that have high cover in midsuccessional stages.

A number of species, although often occurring more frequently in specific successional stages, exhibited high occurrence ($\geq 20\%$) in all stages. These species could be a major component of a plant community at any point in the successional cycle and include cheatgrass, bottlebrush squirreltail, Sandberg bluegrass, tailcup lupine, mountain snowberry, low rabbitbrush, bitterbrush, and desert gooseberry.

Species Variation with Aspect

Species can be grouped according to differences in occurrence on the various aspects. Many root-sprouting shrubs and perennial forbs typically had higher occurrence on north and east aspects (Table 4). Other species associated with east slopes included Indian ricegrass (*Oryzopsis hymenoides*), mutton bluegrass, Thurber needlegrass (*Stipa thurberiana*), and Anderson peachbrush. Holboell rockcress occurred most frequently on north aspects. Many annual forbs were more prominent on south and west slopes than on north and east slopes. Rubber rabbitbrush and cheatgrass exhibited significantly higher occurrence on west slopes than on north or east slopes. South slopes had medium occurrence of these species. Shrubs that regenerate by seed (i.e., big sagebrush and bitterbrush), Hood's phlox (*Phlox hoodii*), and horsebrush (*Tetradymia canescens*) tended to occur least frequently on south slopes and with equal occurrence on other slopes. Most other species, including the two most frequently occurring perennial grasses, Sandberg bluegrass and bottlebrush squirreltail, had no significant differences among aspects.

North and east slope conditions appear to favor the establishment of perennial species. These slopes generally have better moisture relations, less variation in temperature, and generally less harsh conditions than south and west slopes. Conditions limiting the occurrence of annual species may range from reduction of their soil seed reserves from long-term preburn competition by perennial species to the prolonging of the winter dormancy of many winter annuals (Baskin and Baskin 1981), by cooler temperatures and longer snow cover on north and east slopes.

Other site factors appear to determine the establishment patterns on south and west aspects. On these sites, large daily temperature and moisture differentials, especially in spring and early summer, can easily damage susceptible seedlings. Annual species appear to survive these fluctuations better than most perennial species (Evans and Young 1982, Young and Evans 1982). Species that showed no marked preference for aspect appear to germinate and survive equally well under a variety of environmental conditions.

Variation of the Successional Cycle among Aspects

Canopy cover by growth forms reflected and summarized individual species cover

TABLE 5. Percent of relevés with cover values ≥ 5% for five growth forms, two aspect groups, and five successional stages.

	North and east aspects					South and west aspects				
	successional stages									
Growth forms	Early	Early mid	Mid	Late mid	Late	Early	Early mid	Mid	Late mid	Late
Shrubs	${}_{w1}18^{d2}$	${}_{v}71^{b}$	${}_{v}79^{b}$	${}_{v}97^{a}$	${}_{v}49^{c}$	${}_{x}0^{e}$	${}_{w}53^{c}$	${}_{v}76^{b}$	${}_{v}90^{ab}$	${}_{v}47^{c}$
Annual forbs	${}_{v}38^{b}$	${}_{x}2^{d}$	${}_{x}3^{d}$	${}_{y}0^{d}$	${}_{x}4^{d}$	${}_{v}65^{a}$	${}_{x}35^{b}$	${}_{y}11^{c}$	${}_{wx}25^{bc}$	${}_{x}2^{d}$
Perennial forbs	${}_{vw}35^{a}$	${}_{x}20^{b}$	${}_{w}16^{b}$	${}_{v}0^{c}$	${}_{x}6^{c}$	${}_{w}22^{ab}$	${}_{x}20^{ab}$	${}_{y}13^{bc}$	${}_{x}5^{bc}$	${}_{x}3^{c}$
Annual grasses	${}_{y}0^{f}$	${}_{w}56^{b}$	${}_{w}24^{cd}$	${}_{x}16^{de}$	${}_{x}2^{f}$	${}_{x}9^{ef}$	${}_{v}80^{a}$	${}_{w}55^{b}$	${}_{w}45^{bc}$	${}_{x}3^{f}$
Native perennial grasses	${}_{wx}15^{bc}$	${}_{x}19^{b}$	${}_{w}26^{ab}$	${}_{w}42^{a}$	${}_{w}25^{ab}$	${}_{x}0^{d}$	${}_{z}9^{cd}$	${}_{x}32^{a}$	${}_{x}15^{bc}$	${}_{w}14^{bc}$

[1]Percents in a column preceded by the same letters v, w, x, y, or z do not differ significantly at $P < .05$.
[2]Percents in a row followed by the same letters a, b, c, d, e, or f do not differ significantly at $P < .05$.

among successional stages and aspects (Table 5). Early succession on all slopes was dominated by perennial and annual forb cover, with higher perennial forb cover on north and east slopes and higher annual forb cover on south and west slopes. In addition, north and east slopes had high cover of shrubs and native perennial grasses. Early midsuccession brought a sharp increase on all aspects in the number of relevés with shrub and annual grass cover ≥ 5% and a sharp decrease in the same measure for annual forbs. Annual forbs remained an important component on south and west slopes throughout midsuccession, but not on north and east aspects. During all stages of midsuccession, annual grass cover was significantly greater on south and west slopes than on north and east aspects, and perennial grasses tended to be higher on north and east slopes. By late succession, the number of relevés with perennial and annual forb and annual grass cover ≥ 5% decreased on all aspects to less than 6%.

Perennial grass and shrub cover also decreased by late succession but still maintained relatively high cover on all aspects. North and east slopes tended to support higher cover of perennial grasses than did the south and west slopes, but the difference was not significant. Differences between aspect groups were even less for other growth forms. Different moisture, temperature, and light regimes on the different aspects appear to determine the species and subsequently the growth forms that can establish and survive, as well as the speed with which a species or vegetational group becomes prevalent or diminishes. This in turn controls the successional pattern.

Affect of Seeding on Other Species

Eight of the 21 burns were seeded. Dominant seeded species included crested wheatgrass (*Agropyron desertorum*), intermediate wheatgrass (*Agropyron intermedium*), and smooth brome (*Bromus inermis*). Seven of the eight seeded burns were identified as early midsuccessional and midsuccessional stages. The eighth seeded burn, which was only one year old, will not be discussed because seeded species generally appeared only in trace amounts. No consistent pattern emerged when comparing occurrence of shrubs on seed and nonseeded burns (Table 6). Three species had higher occurrence on nonseeded burns, one had higher occurrence on seeded burns, and three exhibited no significant difference between the two groups.

All nonseeded grass species occurred significantly less on seeded burns. This would be expected because most seeded species were grasses selected for their competitive ability. Cheatgrass, however, is a highly competitive grass whose decrease on seeded burns appears to be limited to north and east slopes and high elevation sites, where seeded species have a competitive edge (Koniak 1983). Occurrence of perennial forbs was generally not affected by seeding. Only two species, sulfur buckwheat (*Eriogonum umbellatum*) and Hood's phlox, occurred less frequently on seeded burns. These species are relatively woody and often classified as half-shrubs. Only five annual species occurred on enough midsuccessional sites to examine. Tumble mustard and alfileria occurred less frequently on seeded burns than on nonseeded. The other species showed no significant difference

TABLE 6. Effect of seeding on naturally occurring species.[1]

Species with significantly higher occurrence on nonseeded sites than on seeded sites	Species with no significant differences in occurrence between seeded and nonseeded sites or with greater occurrence (*) on seeded sites
Shrubs	Shrubs
Artemisia tridentata	*Ephedra viridis*
Chrysothamnus nauseosus	*Purshia tridentata* (*)
Chrysothamnus viscidiflorus	*Ribes velutinum*
	Symphoricarpos oreophilus
Grasses	
Bromus tectorum	Grasses
Oryzopsis hymenoides	None
Poa fendleriana	
Poa sandbergii	Forbs
Sitanion hystrix	*Arabis holboellii*
Stipa thurberiana	*Argemone munita* (*)
Agropyron spicatum	*Crepis acuminata*
	Lupinus caudatus
Forbs	*Lygodesmia spinosa* (*)
Eriogonum umbellatum	*Machaeranthera canescens*
Phlox hoodii	*Phacelia hastata*
Sisymbrium altissimum	*Astragalus purshii*
Erodium cicutarium	*Chaenactis douglasii*
	Phlox spp. (perennial species)
	Penstemon speciosus
	Gilia spp. (annual species)
	Mentzelia albicaulis
	Eriogonum spp. (annual species)

[1]Species that occurred on at least two seeded and two nonseeded burns in early midsuccession and midsuccession.

between occurrence on seeded and nonseeded sites.

Seeding appears to be detrimental to a number of naturally occurring species. This should be taken into account when examining the results of this study. However, if percent occurrence in early midsuccession and midsuccession from Table 3 were adjusted to compensate for apparent losses due to seeding, the changes would generally be less than 10%. In addition, other factors may be confounding the apparent decrease in species occurrence correlated to seeding because the burns are of different years and locations. Because of the difficulty in isolating the cause of decreased occurrence on seeded sites and the relatively small decrease involved, it was not considered worthwhile to analyze seeded burns separately from nonseeded.

CONCLUSIONS

Plant succession following wildfire within the pinyon-juniper type has previously been described as relay floristics (Arnold and others 1964, Erdman 1970, Barney and Frischknecht 1974), a sequential migration of later successional species into a site (Egler 1954). Everett and Ward (1984), however, have indicated that initial floristics, the sequential dominance of a site by species on the burn immediately after wildfire (Egler 1954), may be of equal or even greater importance. This study supports the latter hypothesis. Species that became dominant in midsuccession and late succession were present in the early stage. Slow growth or establishment rates precluded early dominance. Tree species, which rely on nurse plants for establishment and survival, were the only exceptions.

Within the pinyon-juniper woodlands, postburn succession may follow multiple pathways (Everett and Ward 1984). Successional patterns varied with aspect and associated preburn species composition. To increase the predictability of postburn plant and community response, effects of elevation, soil type, seeding, postburn climate, and severity and timing of disturbance should also be considered and studied at greater length.

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